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THE RELATIONSHIPS OF THE  
"WREN-THRUSH", ZELEDONIA  
CORONATA RIDGWAY

CHARLES G. SIBLEY





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# THE RELATIONSHIPS OF THE "WREN-THRUSH", *ZELEDONIA CORONATA* RIDGWAY

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## ABSTRACT

Comparisons of the electrophoretic pattern of the egg-white proteins of *Zeledonia coronata* with the patterns of most groups of passerine birds indicate that this species is not a thrush, but a "nine-primaried oscine", probably allied most closely to, and possibly a member of, the wood warblers (Parulidae of Wetmore, 1960). Investigation of the taxonomic history of *Zeledonia* suggests that an early combination of bias, errors, and incomplete comparative studies conspired to divert the attention of later investigators from the ample anatomical evidence indicating the true relationships of *Zeledonia*.

## THE TAXONOMIC HISTORY OF ZELEDONIA: 1888-1905

On November 23, 1888, Señor Anastasio Alfaro, the Director of the National Museum of Costa Rica, collected a small passerine bird at an elevation of 2660 meters, high on the slopes of the Volcán de Poás in Costa Rica. Apparently the bird reminded him of a small thrush for he wrote the generic name *Catharus* on the label. This specimen was sent to Robert Ridgway who selected it as the type of a new genus and species, *Zeledonia coronata* (Ridgway, 1889), dedicated to his friend, Señor José C. Zeledon.

In the original description Ridgway clearly was influenced by Sr. Alfaro's opinion that the bird was a thrush because he began the description of *Zeledonia* by noting that it was "somewhat like *Catharus* . . ." and, later, mentioned that "the loose-webbed rectrices with finely acuminate points, as well as the loosely-webbed remiges, slender bill, and long-booted tarsi with sharp posterior edge remind one of *Catharus gracilirostris*, to which genus Mr. Alfaro, the collector, had referred the bird." However, Ridgway also noted that "the coloration of the head suggests that of *Basileuterus coronatus*. . . ."

Ridgway found the *Zeledonia* had only 10 rectrices and 18 remiges while typical thrushes have 12 and 19 respectively. He noted, however, that *Catharus gracilirostris* has only 18 remiges, apparently not counting the relatively short outer primary in this species. Ridgway also compared *Zeledonia* with *Scytalopus* (Rhino-cryptidae) and *Xenicus* and noted that the tarsi of *Zeledonia* were "faintly scutellate", although described as "booted" and hence thrush-like, earlier in the paper.

Although the collector's designation of the specimen as a *Catharus* apparently provided the original suggestion that *Zeledonia* was a thrush, Ridgway did not assign *Zeledonia* to any family in the original description. Instead he remarked (1889: 537) that "this remarkable new genus is so peculiar in its characters that I am in much doubt as to which family it belongs."

In a footnote to the original description Ridgway (1889:538) reported that F. A. Lucas had undertaken a study of the skeleton of *Zeledonia* and that Lucas had informed him "that so far as his investigations have gone they show that *Zeledonia* is not related to

*Catharus*. . .” This was all that was ever published as a result of Lucas’ study.

Salvin and Godman (1888-97: 248) compared *Zeledonia* with *Basileuterus*, *Xenicus* and *Scytalopus* and concluded that it was probably not related to any of these genera and that “the position of this genus must remain in abeyance pending a full examination of its internal structure.”

The oscinine affinities of *Zeledonia* were established by Pycraft (1901) who examined the syrinx and wing muscles. Pycraft noted, however, that “its exact position had yet to be determined.”

Sharpe (1903: 183), acting upon Pycraft’s discovery that *Zeledonia* was oscinine but apparently also influenced by the early bias toward *Catharus*, placed *Zeledonia* between *Catharus* and *Sialia*. In a footnote, however, he stated that “the correct position of this genus is still unknown.”

In 1905 Pycraft published the results of a more extensive study of the anatomy of *Zeledonia* that was undertaken “to decide, if possible, whether the position assigned to *Zeledonia* by Dr. Sharpe, on the evidence of external characters, was at least approximately correct. . . .” Pycraft examined the external morphology of the bill and legs, the pterylography, the wing and thigh muscles, the syrinx, and the skeleton. His paper appears to be a reasonably definitive study until it is realized that the comparisons were made primarily with various thrushes. A few comparisons with sylviids were noted and other groups are mentioned but there is no evidence that extensive comparisons with many passerine groups were undertaken. Throughout the paper Pycraft lamented the lack of comparative material and the unsatisfactory condition of the only available anatomical specimen of *Zeledonia*. Only skins of most of the thrush genera were available to him and he noted (p. 3) that “these have proved to be of no help whatever in the matter.”

#### A RE-EXAMINATION OF PYCRAFT’S EVIDENCE

Because Pycraft’s paper is the basis for all subsequent opinions concerning the affinities of *Zeledonia* it is important to examine it in some detail. In the following section Pycraft’s principal points are considered, accompanied by comments on certain comparisons I have made.

## BILL AND LEGS

Pycraft (1905: 4) noted that "the nostrils are covered by a membranous operculum having the form of a triangle. So far this operculum appears to be unique." The shape of the ventral margin of the nasal operculum in *Zeledonia*, as noted by Pycraft, is convex with a sharply inflected angle at the point of maximum convexity, thus producing the triangular shape noted by Pycraft. This contrasts markedly with the concave or straight ventral margin in many thrushes. I have examined alcoholic specimens of *Turdus migratorius*, *Sialia sialis*, *Hylocichla ustulata*, *Catharus frantzii*, *Saxicola rubetra*, *Erythropygia leucophrys* and *Erithacus rubecula*. In all except *Erithacus* the ventral margin of the nasal operculum is straight or concave. However, in *Erithacus* there is a noticeable angle, which produces a slightly triangular shape. The effect is to provide an operculum that nearly occludes the nostril, as in *Zeledonia*.

An examination of nasal opercula in the wood warblers reveals a parallel situation. The margin is straight or concave in *Dendroica magnolia*, *Vermivora ruficapilla*, *Wilsonia pusilla*, *Setophaga ruticilla*, *Helmitheros vermivora*, *Oporornis formosus*, *Geothlypis aequinoctialis*, *Seiurus aurocapillus* and *Icteria virens*. In the genus *Basileuterus*, however, there is a tendency to develop a triangular shape. The operculum of *B. culicivorus* has a decided angle, less than in *Zeledonia* but of the same appearance. *B. leucoblepharus* also has an obviously triangular operculum while in *B. rufifrons* there is but a slight indication of the angle.

It is tempting to suggest that the similarity in dorsal coloration between *Zeledonia* and *Basileuterus coronatus*, plus the similarity in the nasal opercula of the two genera, indicates that *Zeledonia* is closer to *Basileuterus* than to other paruline genera. However, the existence of the triangular operculum in *Erithacus* suggests that the shape of this structure is probably correlated with feeding on the ground and perhaps with using the bill to dig and probe. Thus convergence alone may have produced the similar opercular shapes and they may indicate nothing about genetic relationships.

The podotheca was described by Pycraft (p. 7-8) and "found to be formed by the fusion of four separate scutes, traces of which can be distinctly seen." Pycraft went on to discuss the uncertain

taxonomic value of tarsal scutellation and came to no firm conclusion as to its meaning in *Zeledonia*.

The margins of the tarsal scutes can be seen in the alcoholic specimen available to me and Pycraft's description is verified. The tarsus is not truly "booted" but there has been a considerable degree of fusion between the scutes. Presumably this is an adaptive response to life on the ground in the wet, densely vegetated habitat of *Zeledonia*.

#### PTERYLOGRAPHY

Pycraft described the feather tracts of his specimen and confirmed that *Zeledonia* has nine functional primaries and a vestigial tenth. He noted (p. 6) that "according to the usual ornithological custom, this wing would be considered to have but 9 primaries."

In a summary of the "pterylosis of *Zeledonia* and of the Turdidae in general" Pycraft (p. 9) presented the following inconclusive remarks:

In its pterylogical characters *Zeledonia*, so far as I have been able to discover, agrees more nearly with the Turdidae than with any other group.

But what are, precisely, the pterylogical characters of the Turdidae? Unfortunately, owing to lack of material, I cannot at present say, nor can I find any scientific contribution to the subject. So much, however, seems apparent, that the Turdidae, as a group, present certain common characters, which may be regarded as distinctly Turdine. It is possible, however, that these distinctions, which are of a somewhat subtle description, will break down when the pterylosis of the Timaliidae (revised), Pycnonotidae, Alaudidae, Motacillidae, Mnioiltidae, and Sylviidae — of Dr. Sharpe's 'Hand-list' — come to be studied. These several "families" will, I believe, prove to be more closely related than has been supposed.

These statements reveal only that Pycraft was unable to come to any conclusions at all concerning the significance of pterylosis.



## MYOLOGY

"Nothing of importance appears to be derivable from the study of the myology of *Zeledonia*." Following this remark Pycraft commented upon the "typically passerine" wing and thigh muscles and noted various differences and similarities between *Zeledonia* and other genera, mostly thrushes.

## OSTEOLOGY

Careful study of the skull, sternum, and shoulder-girdle of *Zeledonia* leaves little doubt but that this bird must be regarded as one of the Turdidae. The skull, however, presents one or two relatively important features, which may, perhaps, be regarded as primitive characters. . . . The Thrush-like characters of the skull are to be found in the form of the tympanic cavity and of the palate. These points of common resemblance, it must be remarked, by no means leap to the eyes on a first examination, nevertheless they are real. They seem to indicate that *Zeledonia* should be regarded as a primitive Thrush, in the wide sense of the word. . . .

Following this statement Pycraft (p. 14-22) described the tympanic region, palate, and other features of the skeleton of *Zeledonia*. Unfortunately, as for other characters, Pycraft mentioned only a few genera, mainly thrushes, with which he compared *Zeledonia*. In spite of his seemingly confident introductory statement that *Zeledonia* is a thrush he recorded a series of differences between the skeleton of *Zeledonia* and those of the thrushes he used in his comparisons. In each instance Pycraft designated the condition in *Zeledonia* as "primitive" or "specialized" to explain the differences from the thrushes.

It is difficult to judge the validity of Pycraft's statements without assembling the same specimens he used and checking each point. However, it seems clear that he examined material from only a few groups and that most of the osteological characters of *Zeledonia* that he designated as thrush-like are either of wide distribution in the Passeres or actually differ from the condition in the thrushes. For example, Pycraft laid particular emphasis upon the tympanic cavity as being thrush-like in *Zeledonia*. He began by noting the condition in *Menura* and stated (p. 19) that "this

type appears in a large number of widely different groups, and the fact may be regarded as an additional indication of its primitive character."

The turdiform birds, Pycraft went on to say, "appear to have departed from this type along two different lines." These are represented by *Sialia* as the "ground-type" and by *Erithacus*, *Saxicola* and the Sylviidae as the second type. *Zeledonia* is described as having the tympanic region of the skull "specialized in one respect" and "indeed the peculiar features of this region of the skull appear to have resulted from a modification of the type of tympanic region in *Sialia*, not as it is in adult life, but as it appears during its earlier stages of development." Then, in what must be regarded as the death blow to his argument that these characters indicate family level relationships, Pycraft wrote (p. 20): "The skulls of *Anthus* and *Motacilla*, it should be remembered, resemble *Sialia* in the form of the tympanic cavity."

The palatal evidence fares no better. Pycraft described (p. 21-22) and figured (pl. II) the palatal region of *Zeledonia* and noted that "the style-shaped maxillo-palatines of *Zeledonia* represent an undoubtedly specialized condition. In the typical Turdiform palate . . . these structures are larger, spoon-shaped, and inflated at the free end to form a kind of pocket. . . . The linear form seen in *Zeledonia* is obviously a degenerate condition of a maxillo-palatine of the type found in *Erithacus* or *Sialia*, for example."

Pycraft apparently did not compare the maxillo-palatines of *Zeledonia* with those of the nine-primaried oscines. I have compared the palatal regions of the paruline genera *Seiurus*, *Geothlypis*, *Vermivora* and *Helmitheros*, the turdine genera *Hylocichla* and *Sialia* and the illustration of *Zeledonia* in Pycraft's paper (pl. II, 7). It seems clear that the "linear form" of the maxillo-palatines in *Zeledonia* agrees with the condition in the wood warblers and, as noted by Pycraft (p. 22), contrasts markedly with the "larger, spoon-shaped, and inflated" maxillo-palatines of the thrushes.

In his Summary (p. 22-23) Pycraft stated: "as to the precise position of *Zeledonia* I regret that I can say nothing definite until I have had an opportunity of examining much more material than is procurable at present. . . . The specimen submitted to me . . . was so much damaged that reliable data on many questions concerning the soft parts were impossible. . . . Nevertheless, it

seems to me that there can be no doubt about the Turdine affinities of *Zeledonia*. . . . Its nearest allies seem to be among the Sialinae."

#### EVIDENCE AND OPINIONS AFTER 1905

Pycraft's uncertain evidence was apparently ignored thereafter but his conclusion was accepted without further debate. Ridgway, however, went even further. He placed *Zeledonia* in the Turdidae in the manuscript of Part IV of *The Birds of North and Middle America* (1907: 69-72), which was written before Pycraft's 1905 paper appeared; the publication of Pycraft's results prompted Ridgway (1907: 885) to prepare an addendum in which he described the new family Zeledoniidae. His reason for this move was based on the combination of "nine obvious primaries . . . and only ten rectrices! This necessitates the removal of the genus from the Turdidae, and there being no other group into which it can be properly fitted, I propose a new family, Zeledoniidae, for its accommodation. . . ."

From this point on, *Zeledonia* was either placed with the thrushes (Carriker, 1910; Ripley, 1952, 1964; Blake, 1958; Mayr and Amadon, 1951; Beecher, 1953) or the family Zeledoniidae was recognized (Hellmayr, 1934; Eisenmann, 1955; Wetmore, 1960; Slud, 1964).

The only expressed doubts seem to be those of Mayr and Amadon (1951: 18) who noted that the "Turdinae include a number of aberrant genera that . . . may even be wrongly placed with this subfamily. . . . Among these difficult genera [is] . . . *Zeledonia* . . . thought by Sharpe and by Pycraft (1905) to be an aberrant thrush. . . ."

Beecher (1953) discovered additional differences between *Zeledonia* and the thrushes and similarities to the wood warblers but he left *Zeledonia* in the Turdidae. In his study of the jaw muscles of the oscines Beecher found (p. 281) that the typical thrushes have a bifid M. pseudotemporalis superficialis (=M6) with parallel muscle fibers. *Zeledonia*, in marked contrast, has a trifid M6 composed of pinnately arranged fibers. Other groups with a "trifid pinnate M6" include the vireos and the paruline warblers, according to Beecher's descriptions and illustrations (p. 305-307).



## THE EGG-WHITE PROTEIN EVIDENCE

The first known nest of *Zeledonia coronata* was found by Mr. James H. Hunt in April 1968 during his study of the species in Costa Rica. Mr. Hunt collected the first egg that was laid and forwarded the egg white via Mr. William Buskirk to Dr. George H. Lowery, Jr. at Louisiana State University. Dr. Lowery sent the specimen to me and a study of the egg-white proteins of *Z. coronata* was carried out using starch gel electrophoresis. The technique is described in Sibley, Corbin and Haavie (in press).

Comparisons have been made with the electrophoretic patterns of approximately 650 species representing 60 of the 70 passerine families recognized by Wetmore (1960). These include 46 species of thrushes, 47 species of emberizine finches, 18 species of tanagers, 17 species of wood warblers, 30 species of troupials and similar numbers of species in other passerine groups. The complete data will be presented elsewhere (Sibley, in press).

On the basis of these extensive comparisons it is clear that the egg-white proteins of *Zeledonia* are electrophoretically indistinguishable from those of the "nine-primaried oscines" and that they differ from those of the thrushes. The "nine-primaried oscines" and *Zeledonia* have a pattern in which there is a relatively slow component 18, a fast, usually faint, pre-albumin, and an absence of the "ovomucoid" fraction. The thrushes have a strong "ovomucoid" fraction migrating between the ovalbumin and the ovotransferrins and a tendency for the ovalbumin and component 18 to migrate relatively fast. Figure 1 illustrates these similarities and differences.

It is not possible, from the egg-white data alone, to determine to which of the several groups of "nine-primaried" oscines *Zeledonia* should be assigned. In its morphology, however, it seems closest to the wood warblers. The allocation of *Zeledonia* within the nine-primaried assemblage is part of a larger problem that is considered in detail elsewhere (Sibley, in press).

## ACKNOWLEDGMENTS

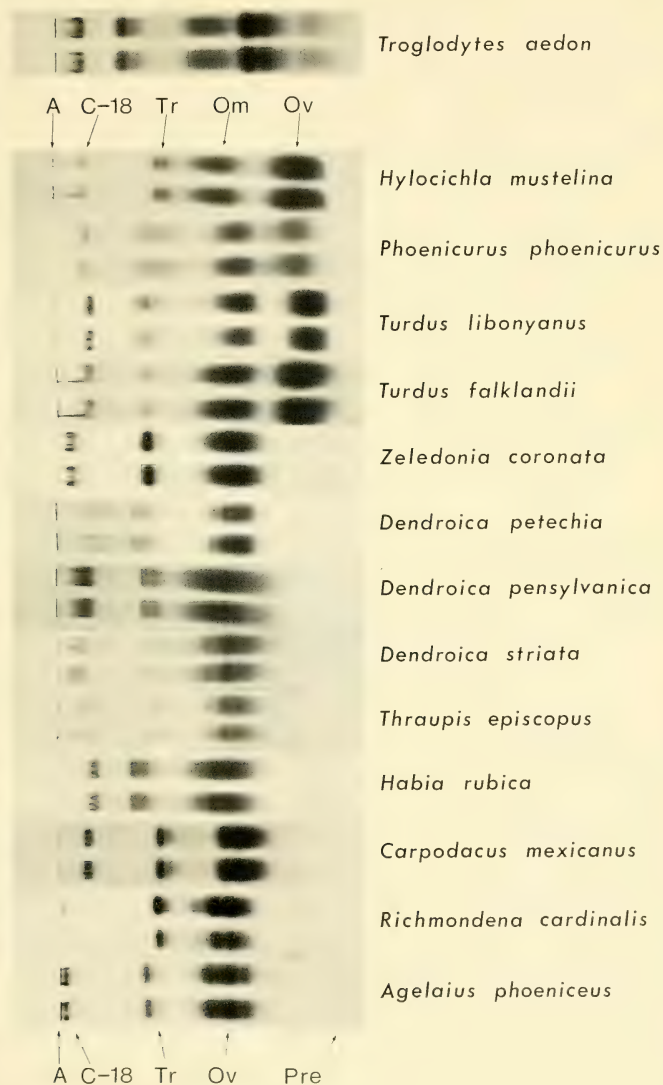
I am grateful to Mr. James H. Hunt, to Mr. William Buskirk, and to Dr. George H. Lowery, Jr., for providing the specimen of egg white of *Zeledonia coronata*. It was due to Dr. Lowery's interest and encouragement that the study of *Zeledonia* was undertaken.

Dr. Kendall W. Corbin, Mr. Jon E. Ahlquist and Dr. N. Philip Ashmole have provided advice and assistance during the study of *Zeledonia* and in the preparation of the manuscript. Dr. Richard L. Zusi permitted me to examine the type and other specimens of *Zeledonia coronata* in the collection of the U.S. National Museum. Lois Robertson assisted with the laboratory work and Georgette Lewis typed the manuscript.

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FIGURE 1. Starch gel electrophoretic patterns of the egg-white proteins of a wren (*Troglodytes*), several thrushes (*Hylocichla*, *Phoenicurus*, *Turdus*), the wren-warbler (*Zeledonia*), and several "nine-primaried oscines" (*Dendroica*, *Thraupis*, *Habia*, *Carpodacus*, *Richmondia*, and *Agelaius*).

The application slots (A) are indicated by the white rectangles at the left ends of the patterns. Component 18 (C-18) is the first band to the right (anodal) of the application slot. The next anodal bands, usually two or three, are the ovoconalbumins or ovotransferrins (Tr). To the right of the conalbumins in the thrushes are two heavily staining areas, in the nine-primaried oscines only one. The first of these bands in the thrushes is possibly an "ovomucoid" (Om), the second one (most anodal) is probably the ovalbumin (Ov). In *Zeledonia* and the nine-primaried oscines the heavily stained area is thought to be the ovalbumin, and the ovomucoid is assumed to be absent. However, in these there is a faint pre-albumin (Pre) which is absent in the thrushes.



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